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# Quiet threats: soft song as an aggressive signal in birds

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Theory suggests that aggressive signals must be costly if they are to be reliable. Recent research in birds has shown, however, that in many species the best predictors of impending attack are low-amplitude vocal signals, soft songs or soft calls, that seem cheap to produce and easy to cheat. This observation leads to two related but separate questions: (1) why use low-amplitude signals to communicate aggressiveness and (2) what maintains the reliability of soft signals of aggression? We review potential answers to both questions and present evidence relevant to each. While some hypotheses are logically sound, others have logical flaws, and most of the hypotheses have yet to be critically tested. One exception is the hypothesis that the reliability of soft signals of aggressiveness is maintained by receiver retaliation, which has been supported by experimental evidence in multiple species. We emphasize the need for further research, particularly to answer the question of why soft song is soft, and outline future research directions.


How reliability, or 'honesty', is maintained in animal communication systems remains a major topic in evolutionary biology (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). Special attention has been paid to signalling in agonistic interactions, given that in these interactions signallers and receivers have directly opposing interests. Theoretical work indicates that aggressive signals can be reliable if they are difficult or impossible to cheat or too costly to bluff (Grafen, 1990; Nur & Hasson, 1984; Zahavi, 1975, 1977).

It is easy to see how aggressive threat signals emphasizing size or strength can be reliable, as in the case of fundamental frequency in the calls of frogs and toads (Davies & Halliday, 1978) and formant spacing in the roars of red deer, *Cervus elaphus* (Reby & McComb, 2003). In these cases, there is a direct physical link between the size of the animal and the characteristics of its display, making the salient display characteristics difficult or impossible to cheat (Maynard Smith & Harper, 2003). It is also well understood that signals that are intrinsically costly to produce can be reliable about signaller traits relevant to their costs (Grafen, 1990); thus, for example, the energetically costly drumming display of a spider is reliable about the physiological condition of the signaller (Kotiaho, 2000). Many of the signals used in aggressive interactions, however, seem to be both physically possible to cheat and relatively low in intrinsic production costs, raising the question of whether they are indeed reliable threat signals, and if so, how their reliability can be maintained.

In this paper, we focus on an example of a threat signal that has been shown to be a reliable predictor of aggression, but that on the surface appears to be both easy to produce and eminently cheatable: low-amplitude, or 'soft', songs and calls in birds. Soft song was first described as an aggressive signal by Margaret Morse Nice in her classic study of the behaviour of song sparrows, *Melospiza melodia* (Nice, 1943). Soft song has since been shown to occur in aggressive contexts in many other species of songbirds as well (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998). Soft vocalizations have also been found to occur during aggression in other taxa of birds (Reichard & Welklin, 2015; Ręk & Osiejuk, 2011), as well as in certain mammals (Brady, 1981; Gustison & Townsend, 2015).

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Interest in soft song as an aggressive signal picked up recently as a result of a study by Searcy and colleagues which found it to be the only signal that reliably predicted attack on a taxidermic mount in the song sparrow (Searcy, Anderson, & Nowicki, 2006), a finding that has since been replicated in a different population of this species (Akçay, Tom, Campbell, & Beecher, 2013; Akçay, Tom, Holmes, Campbell, & Beecher, 2011). Studies have also found low-amplitude vocalizations to be reliable predictors of aggressive escalation in several other bird species, including swamp sparrows, *Melospiza georgiana* (Ballentine, Searcy, & Nowicki, 2008), black-throated blue warblers, *Dendroica caerulescens* (Hof & Hazlett, 2010), corncrakes, *Crex crex* (Rek & Osiejuk, 2011), and brownish-flanked bush warblers, *Cettia fortipes* (Xia, Liu, Alström, Wu, & Zhang, 2013).

In their review of aggressive signalling through birdsong, Searcy and Beecher (2009) proposed three criteria for establishing that a signal used during aggressive interactions (an agonistic signal) is in fact a threat signal: (1) the context criterion: use of the signal must increase during aggressive interactions; (2) the response criterion: receivers should respond to the signal as if it is an aggressive signal; and (3) the predictive criterion: the signal should predict escalation of the interaction if the receiver does not back down. Soft song satisfies all three criteria (see reviews in Searcy, Akçay, Nowicki, & Beecher, 2014; Searcy & Beecher, 2009). Furthermore, of all the presumed vocal signalling behaviours reviewed by Searcy and Beecher (2009), soft song emerged as the only signal that satisfied all three of these criteria based on available evidence. Although a few other vocal signals, most notably song type matching in western (but not eastern) song sparrows, have since been shown to satisfy these criteria (Akçay et al., 2013; Searcy, DuBois, Rivera-Cáceres, & Nowicki, 2013), soft song remains the only aggressive vocal signal that has been shown to be reliable in several different species.

The striking association between soft vocalizations and reliable aggressive signalling in birds raises two related questions. The first is: why are aggressive signals often low amplitude? Is low amplitude an especially advantageous characteristic in a vocal threat, and if so, why? We refer to this as the 'why soft' question. The second question is: what maintains the reliability of soft signals of aggression? That is, how can soft vocalizations be evolutionarily stable as reliable threat signals, given that they are seemingly easy and cheap to produce? We refer to this as the 'why reliable' question. A series of hypotheses has been suggested to answer these questions, with considerable disagreement over which to favour (Akçay & Beecher, 2012; Laidre & Vehrencamp, 2008; Osiejuk, 2011; Searcy, Anderson, & Nowicki, 2008). Some hypotheses address both questions, but others address only one, so it is important to be clear on the conceptual distinction between the two. It is also important to note that many of these hypotheses are not mutually exclusive, even those that address the same question (Table 1).

Before we review the hypotheses on aggressive soft song below, we should note that the scope of our review is limited to aggressive soft songs and excludes soft vocalizations used in courtship. The latter are likely to be under different evolutionary pressures and most of the hypotheses we review below are simply not applicable to courtship soft song. The evolution of courtship soft song is reviewed elsewhere by Reichard and Anderson (2015).

## AVOIDING UNWANTED ATTENTION

The first proposal we consider, the eavesdropping avoidance hypothesis (Dabelsteen et al., 1998), addresses only the 'why soft' question. It is now widely established that animals eavesdrop on interactions between other individuals, both conspecific and heterospecific (McGregor, 2005; Peake, 2005). If being eavesdropped upon is costly, then decreasing the likelihood of eavesdropping by singing at low amplitudes might be advantageous. Whether and how a signaller benefits from minimizing eavesdropping depends on the category of eavesdropper with which it is dealing. We consider two classes of potential eavesdroppers: predators and conspecifics.

Predators and other natural enemies have been shown to locate prey by their auditory signals in a number of systems, including bats feeding on frogs (Tuttle & Ryan, 1981), skuas preying on petrels (Mougeot & Bretagnolle, 2000) and parasitoid flies attacking crickets (Cade, 1975). For birds, it is generally presumed that producing loud vocal signals is dangerous (Hale, 2004; Krams, 2001; Lima, 2009; Mougeot & Bretagnolle, 2000; Schmidt & Belinsky, 2013). These signals may be particularly risky during aggressive interactions when the attention of the singer is occupied by the intruder. Decreasing the amplitude of the song would be a sensible way to decrease the risk of attracting the attention of a predator during an aggressive interaction.

Although this hypothesis has a rather straightforward logic, evidence for it is lacking. The only direct test of which we are aware is Searcy and Nowicki's (2006) study in which they presented song sparrows with two conditions that both involved territorial intrusions simulated using playback of conspecific songs. A simulated intrusion was accompanied in one condition by playback of song sparrow alarm calls, indicating the presence of predators, and in the other by playback of the songs of yellow warblers, *Dendroica petechia*, as a control. The eavesdropping avoidance hypothesis predicts that the birds should increase their use of soft song under increased risk of predation, but what the authors actually found was the opposite: the proportion of soft songs the subjects sang

**Table 1**
Hypotheses to explain the low amplitude and reliability of aggressive soft song

| Hypothesis | Description | Accounts for low amplitude? | Accounts for reliability in predicting attack? | Generalizes to all soft vocalizations? |
|---|---|---|---|---|
| Eavesdropping avoidance (predators) | Singing softly decreases the chances of the signaller being detected by a predator | Yes | No | Yes |
| Eavesdropping avoidance (conspecifics) | Singing softly decreases the chances of a conspecific competitor detecting the interaction | Yes | No | Yes |
| Readiness | Singing softly is a by-product of postures and visual demands necessary for getting ready to attack | Yes | No | No |
| Competing costs | Singing softly decreases the ability of the signaller to keep off intruders/attract females | Yes | Yes | No |
| Vulnerability handicap | Close-range song makes signallers more vulnerable because of the close distance of the signaller to the receiver | Yes | Yes | No |
| Receiver retaliation | Close-range song increases the likelihood of the receiver retaliating aggressively | No | Yes | No |